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AVAILABILITY AND USE OF SHELLS BY INTERTIDAL HERMIT CRABS

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A typical hermit crab protects its soft parts by enclosing them in a gastropod shell. Empty shells are often durable enough that one could provide protection for a crab's entire lifetime. However, crabs choose shells that fit their bodies closely, and crabs cannot continue to grow unless they have a continuous supply of shells [except *Pagurus prideauxi* (Pike and Williamson, 1959) *P. bernhardus* (Jensen, 1975), and numerous other species (Nyblade, 1974) whose shells support colonial organisms that grow continuously forward from the lip of the shell].

If hermit crabs require a continuous supply of shells, then the shell supply rate may influence crab numbers. An opportunity to test this hypothesis arose during long-term studies of snail populations on a rocky shore area, Shady Cove, 0.5 mile north of Friday Harbor Laboratories, San Juan Island, Washington. Between August 1967 and August 1970, 4272 specimens of *Thais lamellosa* and 582 of *T. emarginata* from the 200 m^2 study area were given individually numbered tags (Spight 1974). About 40% of the snails died each year, and as snails died, their tagged shells were acquired by the hermit crabs of the vicinity. The first crab with a tagged shell was found during May, 1968, and progressively more were found in succeeding months. Since the crabs used many of the tagged shells, the crabs provided a valuable means to verify snail deaths, and deliberate censuses of tagged crabs were undertaken. These census data will be examined here for correlations between changes in the rate of shell supply and changes in the portion of the crab population using shells of *Thais*.

Methods

Censuses

Censuses were taken from August, 1967, until May, 1973. Many of the early censuses covered irregular portions of the study area. After 1968 the entire 200 m^2 area of Shady Cove (see map in Spight, 1974) was searched regularly. Two types of searches were conducted: either each portion of the study area was visited once and the number of each shell or snail encountered was noted (note: the word *shell* indicates a shell occupied by a crab; shells occupied by snails are indicated by the word *snail*). Otherwise, each portion of the study area was visited on two consecutive days, and, on each day, all snails and shells encountered were removed. When a shell was removed from the field, it was measured, and the species of crab occupying it was determined. If the shell was intact, it was then returned. If the shell was broken, an intact shell was provided, and the crab was returned to Shady Cove with the new shell.

Population size

One-day censuses usually did not include all of the hermit crabs in the population because only tagged shells were noted. No collections were undertaken specifically to determine the number of untagged shells being used by the crabs. However, shells without tags were counted during some censuses and these counts can be used to estimate how many untagged shells were typically used. The tagged fraction (P) will be expressed as the ratio of the number of tagged shells to the total number of shells collected.

Tagged shells were introduced during 1969. This introduction affected the tagged fraction and, therefore, uncorrected population estimates. The study area was visited six times between May 1 and 14, and on each visit all crabs were removed from a large covered tidepool (K-9). In the laboratory, all crabs wearing tagless shells traded their shells for tagged ones. The crabs with shells of *T. lamellosa* were returned to Shady Cove on May 18, and those with shells of *T. emarginata* were returned on June 18, 1969.

The tagged fractions also reflect the extent of the snail tagging program. All *T. lamellosa* found on the study area from May, 1969 to August, 1970, were either tagged or removed. In contrast, tags were regularly issued to *T. emarginata* from only about a quarter of the study area (C_u of Spight, 1974).

The census data also underestimate the number of hermit crabs because some tagged shells are not seen. The study area was thoroughly searched during consecutive days on 11 different occasions. The total number of tagged shells (N_m) can be estimated with the data obtained. If the same proportion, k, of the shells was found on the beach each day [*e.g.*, (collection of day 1) $= N_1 = kN_m$ and (collection of day 2) $= N_2 = k(N_m - N_1)$], then k can be found from: $k = 1 - N_2/N_1$.

Hermit crab numbers were obtained from 1-day census totals. It was assumed that k of the crabs without tags were found as well as k of those with tags. (Tags are not as obvious as shells, and all shells found were collected to maximize the number of tags found.) Therefore, the total crab population (N_c) for any date can be obtained from $N_c = N_1/kP$. For shells of *Thais emarginata*, overall averages ($k = 0.622$, $P = 0.609$), were used for all dates. For shells of *T. lamellosa,* the same first-day fraction was used for all dates ($k = 0.733$), but different tagged-fractions were used to reflect the effects of shell additions (a separate P calculated for each date, May-October, 1969, and the average figure, $P = 0.717$, for all dates after October, 1969). The separate population estimates for the two shell species were then summed to obtain the total number of hermit crabs.

Shell availability

The number of shells presumed to be available to the crabs is the number of snails seen alive for the last time during the previous census month. The sources of these numbers are given in detail in Spight (1972); actual numbers have been updated here to reflect censuses taken to and including May 5, 1973. Shell availability was calculated as follows (using June, 1969, as an example): 131 individuals of *Thais lamellosa* were seen for the last time during May 1969. Shells of these snails were assumed to have become available to the crabs before June 26

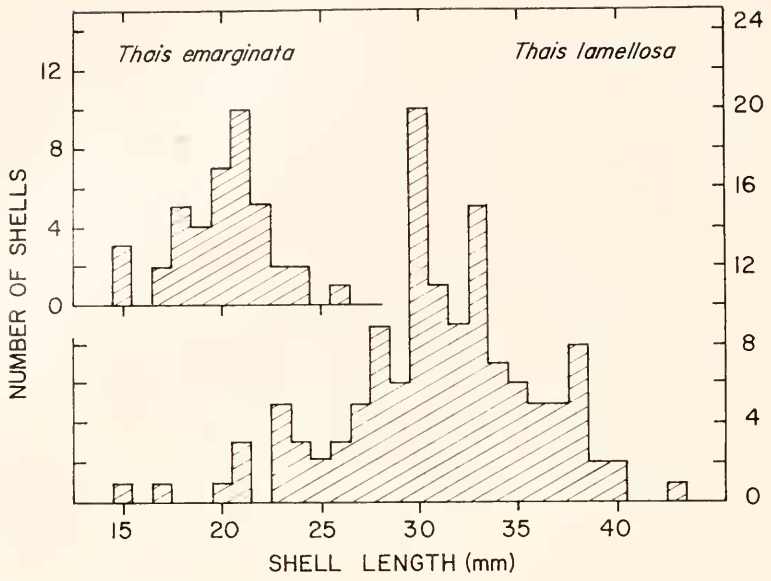

FIGURE 1. Sizes of shells of two snail species. Shells were worn by hermit crabs and were collected on the shore at Shady Cove on September 20, 1969.

(the first snail census date in June) at a rate of 131 shells per 27 days, or 4.8 shells per day. These were available to the 130 crabs present on May 30. Therefore $(4.8 \times 30)/130 = 1.12$ shells per crab-month were available. Based

TABLE I

Sizes of shells used by Pagurus granosimanus *at Shady Cove, San Juan Island, Washington, on various dates. Species determinations were not made on August 5, 1972; all data are included.*

Date	Shell species						Mean total shell length		
	Thais lamellosa Mean shell length			*Thais emarginata* Mean shell length					
	N	mm	s.d.	N	mm	s.d.	N	mm	s.d.
1969									
September 20	129	31.0	4.87	41	20.1	2.41	170	28.4	6.43
November 8	108	30.8	4.94	31	20.9	2.11	139	28.6	6.07
1970									
April 9	42	29.6	5.57	12	20.8	1.64	54	28.7	6.19
July 14	38	29.9	5.99	22	21.2	2.26	88	27.7	6.52
October 15	33	30.4	4.97	12	21.2	2.52	45	27.9	6.05
1971									
April 26	45	28.4	6.19	23	21.1	2.59	68	25.9	6.29
1972									
April 13	8	27.6	2.39	1	22	—	9	27.0	2.92
August 5	10	30.9	7.40	3	21.7	0.58	13	28.5	8.48

on analogous data and calculations, 0.26 shells of *T. emarginata* also became available for a total of 1.38 shells per crab-month.

These numbers exaggerate shell availability. Some shells are crushed when crabs (*Cancer* spp.) kill snails, and others are removed from the study site by birds (Spight, 1976). Other snails may be below the intertidal zone when then they die, and their shells will only become available to intertidal crabs through trades with subtidal crabs. However, as long as snails die in the same ways year after year, snail death rates should be a good index of shell availability. When crabs were counted most frequently, and were most abundant, 60% of available shells were used. Therefore, most snail shells are accessible to intertidal crabs when the snails die.

Results

Shells used

Hermit crabs use the shells of 12 snail species at Shady Cove. Number tags were put on shells of three species of intertidal snails (*Thais lamellosa, T. emargi-*

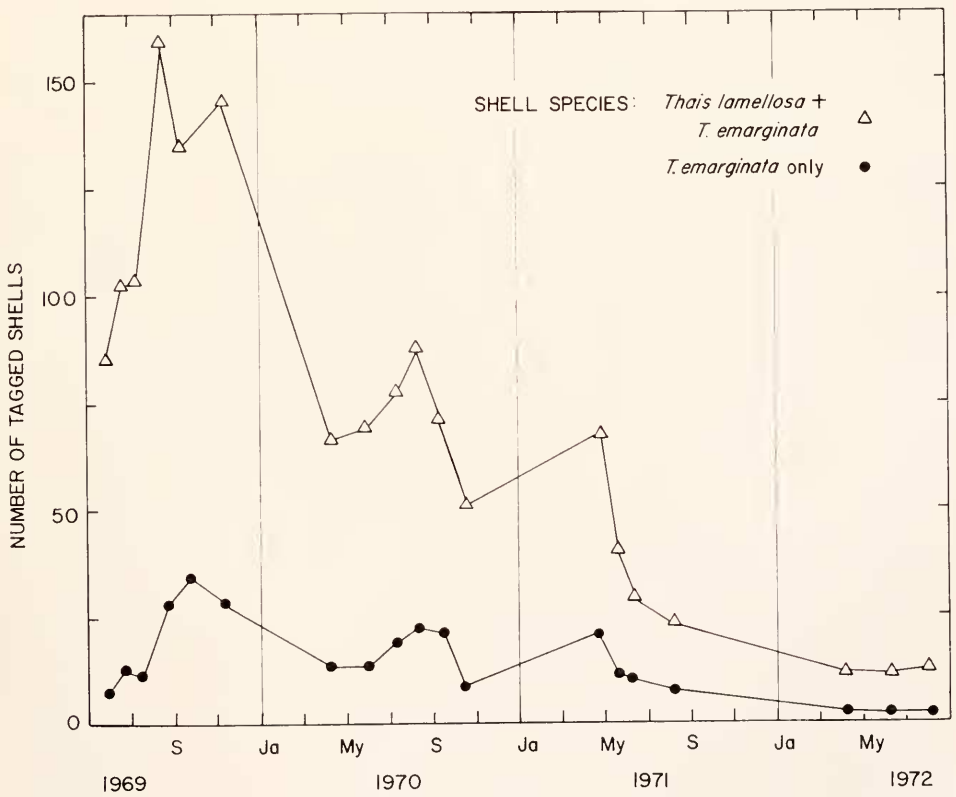

Figure 2. Number of hermit crabs found in tagged shells of *Thais lamellosa* and *T. emarginata,* on various dates, 1969–1972 (first-day only).

TABLE II

Species of hermit crab inhabiting shells of Thais lamellosa *and* T. emarginata *at Shady Cove, San Juan Island, Washington*: *B*, Pagarus beringanus; *G*, P. granosimanus; *and H*, P. hirsutiusculus. *The table includes crabs without tags if these were collected.*

Date of census	Number of crabs inhabiting shells of					
	Thais emarginata			*Thais lamellosa*		
	G	B	H	G	B	H
1969						
September 20–21	41	0	7	132	2	2
October 20	21	0	0	80	0	0
November 8	30	0	8	97	21	4
November 9–11	1	0	0	10	68	0
1970						
April 9–12	23	0	7	64	1	3
July 14	25	0	2	70	5	2
October 15	15	0	5	51	18	2
1971						
April 26	24	0	0	45	2	1
1972						
April 13	1	0	2	8	0	0
Total	181	0	31	557	117	14

nata, and *Searlesia dira*). The crabs used *T. lamellosa* shells 12–47 mm shell length, and *T. emarginata* shells 15–23 mm shell length (Fig. 1). These two shell species provide a vast majority of the shells 15 mm and larger. Tagged *S. dira* shells comprised only 1–6% of the population of tagged shells, and crabs used only a few of the tagged shells that became available; perhaps the crabs avoid the thin *S. dira* shells. Medium to large crabs also use shells of *Margarites pupillus, Calliostoma ligatum, Amphissa columbiana, Bittium eschrichtii, Ocenebra lurida, O. interfossa,* and *T. canaliculata.* Of these species, only *M. pupillus* is abundant at the site, and together these seven shell species provide only a small fraction of the shells (10 mm shell length or more) used by medium to large crabs. The smallest crabs use shells of *Littorina* and *Lacuna* (6–10 mm shell length).

During the present study, only crabs in *Thais* shells were counted, and thus data only provide information on larger hermit crabs. In this paper, the "shell population" includes only *T. emarginata* and *T. lamellosa* shells, even though a few large and all small crabs are excluded.

Most of the crabs in the population were fairly large. *T. emarginata* provided most shells smaller than 25 mm (Fig. 1), but these usually formed only 20–30% of the shell population (Fig. 2). To identify any trends in crab size, mean shell length was calculated for all censuses on which shells had been removed from the field (Table I). The largest and smallest means differ by only 2.8 mm (±5%), and no seasonal or longer term trends are evident. Crabs wearing shells 10–18 mm were never a conspicuous component of the crab population (*e.g.,* Fig. 1).

Species of hermit crabs

Three hermit crab species have been collected at Shady Cove: *Pagurus granosimanus, P. hirsutiusculus,* and *P. beringanus. P. granosimanus* and *P. hirsutiusculus* are generally found under stones during low tide periods. *P. beringanus* does not normally remain in the exposed portions of the tidal zone during low water periods (see also Vance, 1972a). Individuals were occasionally obtained from a covered tide pool (K-9) but were otherwise obtained only by searching at the water line during night low tides (October to February; with the mixed tidal cycle of the San Juan Islands area, the lower shore is generally exposed only once per day).

The relative abundances of these crab species (in *Thais* shells) were obtained by identifying the occupants of all shells removed from the field. Of the 900 crabs

TABLE III

Percentage of the hermit crabs from Shady Cove that were wearing tagged shells. An entry is included for all dates on which shells without tags were noted on the data books. The collection total for a province is included only if untagged shells were noted.

Date of census	*Thais lamellosa* shells		*Thais emarginata* shells	
	Number seen	Per cent with tags	Number seen	Per cent with tags
1969				
May 1	63	61.9	2	50.0
May 1–14	105	55.2	17	41.1
June 18	77	96.1		
July 1	10	70.0		
July 11–17	96	93.7		
July 29	77	88.3		
August 26	67	85.0	25	88.0
September 20–21	177	77.4	72	66.7
October 20	88	84.0	29	65.5
November 8–9	196	69.8	73	46.5
December 8	12	75.0		
1970				
April 9	95	65.2	34	61.7
May 23	40	70.0	10	50.0
May 31	43	76.7		
June 16	34	79.4	3	33.3
July 14	76	75.0	25	56.0
October 15	70	75.7	17	76.4
1971				
April 3	24	70.8	2	50.0
April 26	38	71.0	30	60.0
May 12	33	75.7	10	80.0
May 23	24	75.0	11	63.6
June 7	15	66.7		
1972				
April 13	5	60.0		
1973				
May 4	6	33.3	20	5.0
Total	1402	76.3	35.8	60.9

identified, 82% were *Pagurus granosimanus,* 13% were *P. beringanus,* and 5% were *P. hirsutiusculus* (Table II). The crabs used the two shell species in different proportions. *P. hirsutiusculus* was found disproportionately more frequently in shells of *T. emarginata* (*e.g.,* the smaller shells; Fig. 1), and *P. beringanus* was found only in shells of *T. lamellosa* (*e.g.,* the larger shells; Table II). This usage pattern may reflect shell size rather than shell-species; it parallels the observations of Vance (1972a). The conclusions of this paper are thus based primarily on data for *P. granosimanus.*

Population changes

Many more tagged shells were found on the study area at some times than at others. The crab population doubled between May and August, 1969, and numbers remained high through the fall of 1969. Numbers declined abruptly during the winter, and the decline progressed more or less continuously until the end of the observation period (Fig. 2). In the final census of May, 1973, only 26 crabs were observed, of which only 3 wore tagged shells.

The crabs used untagged shells as well as tagged ones. Overall, about 76% of the shells of *Thais lamellosa* and about 61% of the shells of *T. emarginata* encountered on censuses were tagged (Table III). For *T. lamellosa* shells, the tagged fraction rose from 62% to 96% after the addition of shells in May, 1969, and then gradually decreased to around 70% (mean, for all dates, November 1969 to April, 1972, 71.7%). In June, 1969, 19 shells of *T. emarginata* were added

TABLE IV

Number of hermit crabs in tagged shells found on consecutive searches at Shady Cove.

Date	Total number of crabs found			
	Crabs in *Thais lamellosa* shells		Crabs in *Thais emarginata* shells	
	First day	Second day	First day	Second day
1969				
April 16	18	1	3	0
July 11	92	20	12	2
September 20	100	39	35	16
November 9	118	37	28	9
1970				
April 9	54	10	13	10
July 14	59	22	19	8
October 15	42	10	9	5
1971				
April 26	48	7	20	4
1972				
April 13	10	0	2	0
August 5	11	2	2	0
1973				
May 4	2	0	0	0
Total	554	148	143	54

TABLE V

Estimated crab population and number of shells available. Census totals are numbers of crabs seen on first-day censuses, given by shell species (L, Thais lamellosa; E, T. emarginata). Estimated crab population includes untagged shells of these two snail species (see text). Number of shells available is based on the number of snails seen for the last time on the date listed, the number of crabs seen on that date, and the number of days to the next date; it is given for each shell species.

Date	Number of crabs seen on census		Estimated crab population	Number of shells available per crab per month		
	L	E		L	E	Total
1969						
May 30	78	7	130	1.12	0.26	1.38
June 26	90	13	162	0.67	0.12	0.79
July 11	92	12	166	0.73	0.26	0.99
August 25	132	28	286	0.49	0.14	0.63
September 20	100	35	268	0.63	0.07	0.70
November 8	118	28	298	0.15	0.01	0.16
1970						
April 11	54	13	136	0.78	0.11	0.89
May 31	55	14	142	0.68	0.25	0.93
July 14	59	19	162	0.69	0.23	0.92
August 12	65	23	185	0.65	0.12	0.77
September 10	50	21	151	0.36	0.16	0.52
October 15	42	9	104	0.08	0.02	0.10
1971						
April 26	48	20	144	0.88	0.08	0.96
May 23	29	11	84	0.45	0.02	0.47
June 7	20	10	64	0.41	0.03	0.44
August 5	16	7	49	0.01	0.00	0.01
1972						
April 13	10	2	23	1.36	0.02	1.38
June 9	10	2	23	0.95	0.00	0.95
August 5	11	2	26			

to the 13 known to have been in the population, and the tagged fraction subsequently rose from 41% to 88%. The tagged fraction dropped abruptly to 67% in September, and remained at about that level until May, 1971 (Table III). The lower tagged fraction for *T. emarginata* shells reflects the lower proportion of tagged snails on the study area (see Methods).

Not all of the tagged shells were seen on every census. Overall, 21% of the shells of *T. lamellosa* and 27% of the shells of *T. emarginata* were found on the second day's search (Table IV). These data indicate that 73% of the tagged *T. lamellosa* shells at large and 62% of the tagged *T. emarginata* shells at large were seen on the average census ($k = 0.733$ and 0.622, respectively; see Methods).

The untagged shells and tagged shells that were missed together amount to almost as many as were included in the first-day counts of tagged shells (Table V).

Availability and use of shells

During most months, 0.5 to 1 new shells became available for each crab in the population (Table V). Overall, 24% of the *T. emarginata* shells and 40%

TABLE VI

Availability (snail deaths, or number of snails seen alive for the last time during the month indicated) and use of shells of two snail species by hermit crabs of Shady Cove, San Juan Island, Washington. All snails dying before or not encountered during the final census, May, 1973, are listed as deaths in August, 1972.

Month	*Thais lamellosa*			*Thais emarginata*		
	Snail deaths	Shells used	Per cent	Snail deaths	Shells used	Per cent
1967						
August	1	0	0	0	—	—
September	20	4	20	13	1	8
October	8	2	25	16	1	6
December	16	3	19	4	3	75
1968						
January	5	1	20	0	—	—
February	14	7	50	0	—	—
April	82	27	33	5	2	40
May	42	18	43	10	4	40
June	95	46	48	8	2	25
July	73	42	57	10	2	20
August	142	48	34	63	25	40
September	104	35	35	8	5	62
October	118	56	47	16	2	12
November	15	7	47	19	1	5
1969						
January	4	4	100	0	—	—
April	116	25	22	11	3	27
May	131	61	46	31	15	48
June	54	19	35	10	7	77
July	183	70	38	65	35	54
August	121	33	27	35	24	69
September	278	35	13	29	15	52
November	233	11	5	14	3	21
1970						
April	176	30	17	25	6	24
May	54	20	37	17	4	23
June	87	24	28	35	13	37
July	108	17	16	36	21	58
August	117	13	11	22	8	36
September	63	7	11	29	4	14
October	55	7	13	12	3	25
1971						
April	114	7	6	11	4	36
May	19	0	0	1	0	0
June	52	2	4	4	1	25
August	5	1	20	0	—	—
1972						
April	60	1	2	1	1	100
June	42	0	0	0	—	—
August	169	1	1	0	—	—
Total	2976	684	23	560	215	38

TABLE VII

Observed use of Thais *shells by hermit crabs at Shady Cove as a function of the number of censuses in the months following the death of the snail.*

Shell species	*Thais lamellosa*				*Thais emarginata*			
Number of censuses taken within two months of snail disappearance	0	1	2	3	0	1	2	3
Number of months of observations	5	7	10	7	5	7	10	7
Number of shells available	293	327	1100	895	26	70	238	188
Percentage of shells used	6.5	22.3	27.1	27.4	23.1	12.9	41.5	50.0

of the *T. lamellosa* shells that became available from May 1969 through April 1972 are known to have been used by the crabs (Table VI). More of the available shells were used during 1969 than during later years.

The use frequencies reflect both census frequency and crab population size. More uses were detected when several censuses were conducted shortly after the death date (*e.g.,* 1969; Table VII). Available shells were more often used when many crabs were on the study area (Fig. 3).

DISCUSSION

Hermit crab populations are believed to be limited by shell supplies by many marine biologists. Four kinds of data have been presented to support this hypothesis. First, all accessible shells are occupied; no empty shells are available

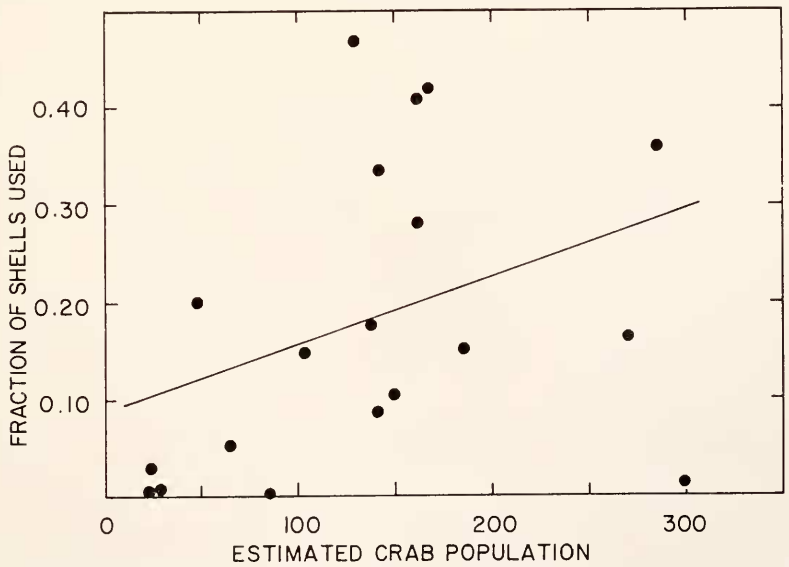

FIGURE 3. Shell use by hermit crabs: use of available shells at different crab densities.

to provide protection for additional crabs (Provenzano, 1960; Childress, 1972). Secondly, many crabs have small or broken shells which they will readily trade for larger or unbroken shells (Vance 1972b). Thirdly, larger crabs become abundant when larger shells become available (Drapkin, 1963). Fourthly, crab populations have increased when shell supplies have increased (Vance, 1972a). Conspicuously absent from this list are any references to the normal components of arguments about population limitation: measurements of the availability of resources (the rate of shell supply) or of crab population parameters (growth or reproductive rates). Furthermore, each of the existing kinds of data provides, at best, ambiguous support for the proposition.

In most environments, the number of shells will be equal to the number of hermit crabs because unoccupied shells are removed by physical processes. Empty shells will roll down the shore until they reach pockets of soft or loose sediment. The shells will then be buried by the shifting sediment and will no longer be available to crabs. Hermit crabs compete with this physical removal and are virtually the only means for keeping a shell on the surface. Therefore, available shells cannot be more numerous than hermit crabs in most communities.

Most crabs would avoid using a small or a broken shell if an alternative were available and have good reasons for doing so. Crabs in inadequate shells are more susceptible to predators (Vance 1972b), produce fewer eggs (Childress, 1972), and grow more slowly (Markham, 1968; Nyblade, 1974). If crabs use poor shells, then good shells must be in short supply, and survival, growth and reproduction may be limited by the number of high-quality shells available. Drapkin (1963) provides a clear example of this type of shell limitation. When a larger shell species became available in the Black Sea (*Rapana bezoar*), its shells were readily accepted by the small hermit crabs then present, and hermit crabs began attaining sizes that had not been seen prior to the introduction. The best estimates of shell adequacy for whole populations are those of Vance (1972a); most large crabs from his population preferred shells larger than their own. None of these examples show that crab numbers are limited by shell supply. In Vance's study, unoccupied small shells were found in nearby tidepools; if these shells were available to crabs, then recruitment and density were not limited by the shell supply. Most larger crabs had inferior shells, and presumably were producing fewer gametes than if better shells had been available. However, Nyblade's (1974) settlement experiments indicate that small shells would be used as long as they are accessible to the larvae.

Vance (1972a) attempted to increase crab numbers on a small isolated reef by adding 12,000 shells. This experiment provides some of the most compelling evidence for shell limitation available to date. However, the rate of increase was low (0.094 crabs per shell added), the experiment was unreplicated (the scale of the effort precluded replication), and year-to-year changes in unmanipulated natural populations have not been typified. Since typical rocky shore populations vary greatly (Spight 1974), Vance's result could well have arisen by chance.

The present data allow a different approach to the shell-limitation problem. A hermit crab (*Pagurus granosimanus*) population was monitored over a relatively long time (Fig. 2). Over the same period, death rates of the snails that furnished the shells were monitored. Changes in the crab population can be compared with changes in shell availability.

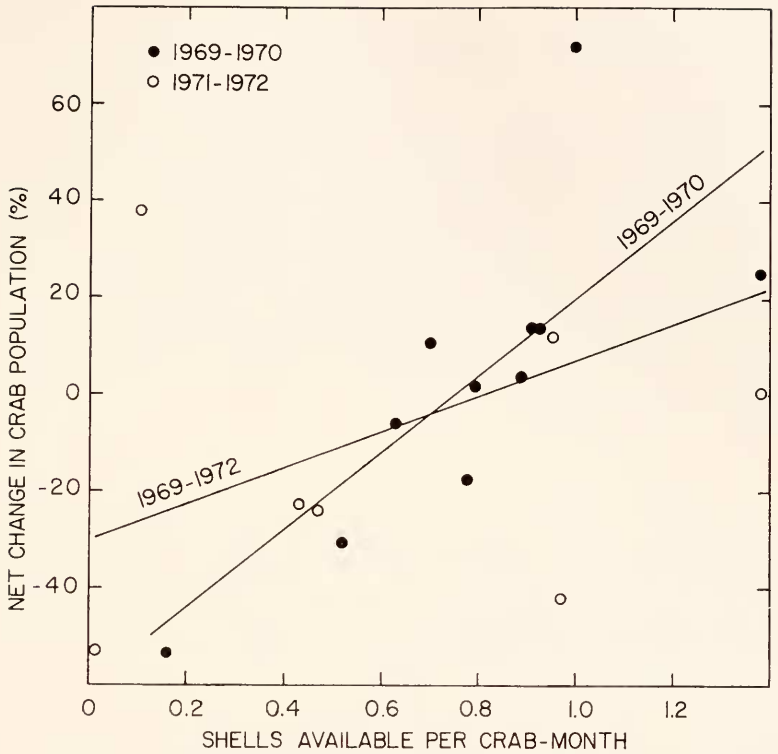

FIGURE 4. Observed changes in the crab population related to the number of *Thais* shells that became available during the period.

The shell supply changed seasonally. Many new shells became available during the spring and summer, and few were available during the winter (Table VI). These seasonal pulses in shell availability were reflected in 1969 and 1970; the crab population increased during summer and fall and decreased during winter.

Shell supplies also changed over the longer term. The snail populations at Shady Cove declined almost continuously during the period of study (Spight, 1972). Correspondingly, crab numbers also declined steadily after reaching a peak in 1969 (Fig. 2). These parallel courses in crab and snail populations are consistent with the hypothesis that crab numbers are affected by the shell supply.

Crab population size was related more directly to shell availability by plotting the net change in the crab population ($N_{t+1} - N_t$, from Table V) against the rate of shell availability (number of new shells per crab-month, from the crab population of Table V, and the number of snails seen for the last time, Table VI). When numbers were changing greatly (1969–1970), variations in shell supply accounted for 59% of the variations in crab numbers ($r^2 = 0.59$; Fig. 4). The correspondence is less for the whole period (1969–1972; $r^2 = 0.21$; the crab population increased overwinter, 1970–1971, and decreased the following spring, while shell supplies should have fostered changes in the opposite direction). The data of Figure 4 indicate that under the conditions at Shady Cove, *Pagurus*

granosimanus numbers will remain constant as long as 0.75–0.80 shells become available for each crab in the population during each month. This is similar to the result of Vance (1972a) and adds further support to his interpretation of his results.

These data support the shell-limitation hypothesis. However, they shed no light upon the actual population processes that lead to the close correspondences observed (Fig. 4). In particular, the constant size structure of the crab population is difficult to reconcile with the large changes in population size. Large changes in population size are usually accompanied by changes in size or age structure (Schaffer and Tamarin, 1973). However, small crabs (in 10–18 mm shells) were not abundant before the population increased, nor were larger crabs more abundant afterwards (Table 1). To confirm the hypothesis, studies of actual crab population processes (De Wilde, 1973; Nyblade, 1974) must be combined with those of shell availability.

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Summary

During a six-year period, several thousand intertidal snails, *Thais lamellosa* and *T. emarginata,* were given individually numbered tags and times of death were noted. These snails provided most of the shells used by intertidal hermit crabs (primarily *Pagurus granosimanus*). Therefore changes in the hermit crab population can be related to shell availability. The crab population increased greatly during 1969, and then declined steadily until the end of the study (1973). Changes in the crab population were highly correlated with shell availability. This hermit crab population will remain constant in size if 0.8 shells become available for each crab each month.

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